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Limits to water transport in *Juniperus osteosperma* and *Pinus edulis*: implications for drought tolerance and regulation of transpiration

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Summary

1. An air-injection method was used to study loss of water transport capacity caused by xylem cavitation in roots and branches of *Pinus edulis* (Colorado Pinyon) and *Juniperus osteosperma* (Utah Juniper). These two species characterize the Pinyon–Juniper communities of the high deserts of the western United States. *Juniperus osteosperma* can grow in drier sites than *P. edulis* and is considered the more drought tolerant.

2. *Juniperus osteosperma* was more resistant to xylem cavitation than *P. edulis* in both branches and roots. Within a species, branches were more resistant to cavitation than roots for *P. edulis* but no difference was seen between the two organs for *J. osteosperma*. There was also no difference between juveniles and adults in *J. osteosperma*; this comparison was not made for *P. edulis*.

3. Tracheid diameter was positively correlated with xylem cavitation pressure across roots and stems of both species. This relation suggests a trade-off between xylem conductance and resistance to xylem cavitation in these species.

4. During summer drought, *P. edulis* maintained higher predawn xylem pressures and showed much greater stomatal restriction of transpiration, consistent with its greater vulnerability to cavitation, than *J. osteosperma*.

5. These results suggest that the relative drought tolerance of *P. edulis* and *J. osteosperma* results in part from difference in their vulnerability to xylem cavitation.

Key-words: Hydraulic conductance, Pinyon–Juniper communities, stomatal regulation, xylem cavitation

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Introduction

Pinyon–Juniper communities are found throughout the high deserts of the south-western United States, predominantly at elevations between 1500 and 2000 m (Johnston 1994). The Pinyon–Juniper habitat is semi-arid, receiving c. 40 cm of yearly precipitation. The actual rainfall over a local elevational gradient, however, can vary more than twofold (West 1988). Juniper dominates in the lower, drier sites and with increasing elevation (and precipitation) community structure shifts to dominance by Pinyon (Woodbury 1947; Woodin & Lindsey 1954; Padien & Lajtha 1992; Lajtha & Getz 1993). As a result, Juniper is generally accepted as the more drought-tolerant species, intermixing with desert flora at the lower end while Pinyon gives way to montane conifers at the higher altitudes.

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This study addresses the vulnerability to xylem cavitation of *Juniperus osteosperma* Engelm. (Cupressaceae) (Utah juniper) and *Pinus edulis* (Torr.) Little (Pinaceae) (Colorado Pinyon Pine), and its relationship to the relative drought tolerance of these two species. Characterizing cavitation in xylem conduits is potentially important for understanding the water stress response of a plant. Thermodynamics of water movement require that if a plant is to continue extracting water from a drying soil, the water potential of the xylem sap must be below that of the soil and decrease in concert with the soil as it dries. As a result, xylem water is typically under tension (absolute negative pressure) and considerably so in xeric environments during drought. Below the vapour pressure of water (2.3 kPa at 20 °C), xylem sap is in a metastable state and at a certain critical pressure an ‘air seed’ can be pulled into the xylem conduit across a pit membrane (Zimmermann 1983; Crombie, Hipkins & Milburn 1985; Sperry & Tyree 1990; Cochard, Cruziat & Tyree 1992), which provides a nucleation site for the formation of water vapour, resulting in a gas-filled conduit. This process is termed xylem cavitation.

Resistance to xylem cavitation potentially confers drought tolerance because maintenance of water filled and functional xylem elements during drought ensures efficient supply of water to evaporation sites in leaves. The greater the cavitation resistance, the higher the gas-exchange rate and the greater the potential for extracting water from a drying soil. In many species, the roots are more vulnerable to cavitation than stems (Sperry & Saliendra 1994; Alder, Sperry & Pockman 1996; Hacke & Sauter 1996). In such a situation, roots may be the first to fail during drought, so that drought tolerance may be related more to the cavitation resistance of roots than stems. Differences in cavitation resistance also have been found between adults and juveniles of the same species, with the more drought-prone juveniles being more resistant than adults (Sperry & Saliendra 1994).

If cavitation resistance confers increased fitness, especially in arid environments, why do plant species vary so widely in vulnerability to cavitation? This may result, in part, from a trade-off between xylem conductance and cavitation resistance. Tyree, Davis & Cochard (1994) show statistically that vulnerability to cavitation increases with increasing conduit diameter and thus conducting capacity. This relation was weak, however, owing to the lack of a necessary link between pit membrane porosity, the actual parameter associated with cavitation, and conduit diameter.

We hypothesized that the superior drought tolerance of *J. osteosperma* compared to *P. edulis* would correspond to a difference in vulnerability to xylem cavitation. Furthermore, we hypothesized that branches and roots within a species would differ in vulnerability to cavitation and that the relative risk of xylem cavitation for these two species would correspond to stomatal regulation of transpiration and xylem pressure. We tested these hypotheses by a combination of laboratory measurements of cavitation vulnerability and xylem anatomy, and field measurements of xylem pressure and transpiration.

Materials and methods

PLANT MATERIAL

Plant material for determining vulnerability to cavitation was collected at two sites, Lake Fork Canyon, 28 km south-east of Spanish Fork, UT (1830 m elevation, 111° 25'W 39° 56'N), and at the mouth of Big Cottonwood canyon, 18 km south of the University of Utah (1520 m elevation, 111° 47'W 40° 38'N). Root segments were cut from lateral roots running nearly parallel with the soil surface at depths of 30–40 cm. Root diameters were 0.4–0.6 cm and branch diameters were 1.1–1.6 cm. Stem and root segments were sampled in lengths of 30 cm or more and were immediately bagged after sampling to minimize dehydration during transport. *Juniperus osteosperma* juveniles were less than 1.0 m tall. Bagged plant samples from

the field were taken to the laboratory and at least 5 cm was cut off each end while under water, eliminating air filled tracheids and leaving segments 20 cm in length for determining the vulnerability curves.

VULNERABILITY CURVES

A vulnerability curve shows the relationship between xylem pressure and the loss of hydraulic conductance via cavitation. The air injection method we used to produce vulnerability curves has been shown to simulate the process of cavitation accurately for a variety of different species (Sperry & Tyree 1990; Sperry & Saliendra 1994; Alder *et al.* 1996), including conifers (Sperry & Ikeda 1997). This method is based on the principle that the critical pressure difference at which air will be aspirated into xylem conduits, which *in vivo* is produced by negative pressure inside the xylem, can be instead generated by positive pressure outside the conduits. Sperry & Saliendra (1994) give a detailed explanation of the experimental procedure. Briefly, the newly cut 20 cm segments were placed in a two-ended pressure bomb and the hydraulic conductance (k) was measured where k ($\text{kg m s}^{-1} \text{MPa}^{-1}$) is equal to the mass flow rate of water through the segment (kg s^{-1}), times the plant segment length (m), and divided by the hydrostatic pressure head causing flow through the segment (MPa). After the initial measurement of k , the bomb pressure was increased in increments of 1.0 MPa, forcing air into the xylem conduits. After a 10 min exposure to an injection pressure, k was remeasured. Previous experiments have shown that 10 min is sufficient to saturate the response at that particular pressure and that exposure beyond this does not further change k (Sperry & Saliendra 1994). The conductance at each air injection pressure was expressed as a percentage loss of the initial conductance and was plotted vs the negative of the air injection pressure. To determine mean cavitation pressure, we replotted vulnerability curves as the loss of hydraulic conductance per unit pressure change (rather than plotting the cumulative loss of conductance) and took the mean of this distribution based on the mid-point of each pressure change.

TRACHEID DIAMETERS

After vulnerability curves were completed, root and branch segments were cut at their mid-points, hand-sectioned and mounted for viewing under a light microscope. Transverse sections were divided into four 90° radial sectors and the diameters of 50 tracheids within each sector were measured in the most recent growth ring (200 measurements per segment). Measurements were made using a drawing tube and bit pad (Micro-Plan II, Donsanto Corp., Natuck, MA, USA) and tracheid cross-sections were approximated as perfectly circular. Tracheids were grouped into 5 µm diameter classes and their contribution to the

total conductance was calculated based on the Hagen–Poiseuille equation (Zimmermann 1983; Nobel 1991), which states that the hydraulic conductance of individual cylinders is proportional to their diameter raised to the fourth power. The hydraulically weighted mean diameter for each segment was calculated as the sum of all diameters to the fifth power divided by the sum of all diameters to the fourth power.

XYLEM PRESSURE AND LEAF TRANSPIRATION

Measurements were made at the beginning (May) and end (August) of the annual summer drought at four field sites in Utah and northern Arizona (including the Lake Fork site described above) to assess the response of xylem pressure and stomatal conductance to drought. The three additional sites were near Zion National Park, UT (112° 53' W 37° 17' N), Grand Canyon National Park, AZ (112° 10' W 36° 2' N), and Pinedale, AZ (110° 11' W 34° 17' N).

All measurements were made on adult plants. Predawn and midday xylem pressures were measured with the pressure chamber ($n = 3\text{--}4$ plants per species). Leaf gas exchange was measured ($n = 3$ plants per species) with a Li-Cor 6200 portable gas-exchange system (Li-Cor, Lincoln, NE, USA). Transpiration rates within the cuvette of the Li-Cor 6200 were used to estimate *in situ* rates of transpiration. The stomatal conductance of these small-leaved trees ($< 0.2 \text{ mmol m}^{-2} \text{ s}^{-1}$) is typically much less than the boundary layer conductance (c. $1.5 \text{ mmol m}^{-2} \text{ s}^{-1}$) even under low wind velocities (Nobel 1991). As a result, the total leaf conductance is closely approximated by the stomatal conductance, regardless of boundary layer conditions. In addition, errors that arise from miscalculation of vapour pressure deficit owing to inaccurate measurement of leaf temperature are minimized in low-humidity environments and small-leaved plants. A large 2 °C error in measurement of leaf temperature at 30% relative humidity causes only a 16% error in calculation of E . In any regard, our use of the Li-Cor 6200 to measure E is chiefly to draw comparisons between the two species, not necessarily to measure absolute values of *in situ* transpiration.

The *in situ* loss of xylem conductance from cavitation was predicted from vulnerability curves of the xylem and field measurements of xylem pressure. The *in situ* xylem pressure was estimated as the mid-point between predawn and midday shoot xylem pressure. This corresponds to the xylem pressure at the hydraulic mid-point of the soil-to-leaf continuum where hydraulic conductance to bulk soil and to transpiring leaf surface is equal. This 'midpath' xylem pressure is probably a better estimate of xylem pressure in the larger roots and branches where vulnerability to cavitation was measured than either predawn or midday shoot values.

Results

Pinus edulis branches had a mean cavitation pressure of -4.50 ± 0.25 MPa (mean \pm SE) which was over 2 MPa less negative than -6.56 ± 0.34 for *J. osteosperma* branches (Fig. 1a; statistical analyses throughout were carried out using one-way ANOVA, followed by multiple pairwise comparison with the Student–Newman–Keuls method or by Student's *t*-test, as appropriate; significance level 0.05 or less unless noted). A mean cavitation pressure of -2.97 ± 0.22 MPa for *P. edulis* roots was also significantly less negative than -6.04 ± 0.71 for *J. osteosperma* roots (Fig. 1b). Within-species comparisons showed *P. edulis* roots were more vulnerable than branches but *J. osteosperma* roots and branches were not different (Fig. 1). *Juniperus osteosperma* juvenile branches (-6.31 ± 0.45 MPa) were not significantly different from adult branches of the same species (Fig. 1a). Differences in the vulnerability curves of *P. edulis* and *J. osteosperma* branches were not apparent until pressures below -4.0 MPa (Fig. 1a). The curves of *P. edulis* and *J. osteosperma* roots, however, were significantly different at all pressure values (Fig. 1b). At a xylem pressure of -6.0 MPa, *P. edulis* had essentially lost all hydraulic conductivity in both roots and branches, whereas *J. osteosperma* at this pressure had an average loss of only 26.7 and 49.4% in its branches and roots, respectively.

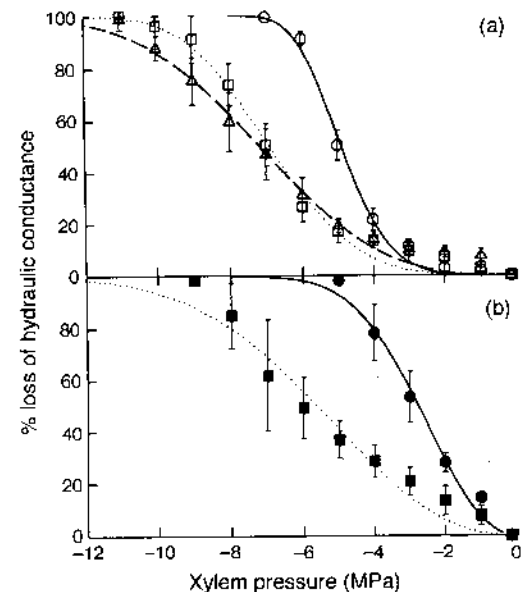


Fig. 1. Loss of hydraulic conductance at decreasing xylem pressures estimated with the air-injection technique. Data is fit with Weibull function [$\% \text{ Loss} = 100(1 - e^{-(P/b)^c})$]. *Pinus edulis* branches (\circ , $b = 5.23$, $c = 5.32$) and roots (\bullet , $b = 3.26$, $c = 2.21$), *Juniperus osteosperma* adult branches (\square , $b = 7.52$, $c = 4.22$) and roots (\blacksquare , $b = 6.56$, $c = 2.37$), and *J. osteosperma* juvenile branches (\triangle , $b = 8.04$, $c = 3.13$). Data points are the average of multiple plant segments where $n = 5$ for each group except *J. osteosperma* juveniles ($n = 7$) and *J. osteosperma* roots ($n = 3$). Error bars are SE.

The estimated contribution of each tracheid diameter class to the total hydraulic conductance is shown in Fig. 2. In general, tracheids were widest in the roots and narrowest in the branches of both species. *Juniperus osteosperma* juvenile branches had a large population of tracheids in the 7.5 μm class, contributing 51% of its total conductance, but otherwise were similar to *J. osteosperma* and *P. edulis* adult branches. Greater than 85% of the hydraulic conductance in branches of these three groups is owing to tracheids in the 7.5 and 12.5 μm diameter classes (5–15 μm). Of the stem groups, only *P. edulis* stems had significant conductance owing to tracheids in the 17.5 μm size class, contributing 13% of its total conductance. Of the five groups studied, root tracheids of both species had the most variable diameters. The wide breadth of tracheid sizes in *P. edulis* roots was a result of interindividual variation in tracheid diameter (see Fig. 3), whereas the variation in *J. osteosperma* was a result of variation within individuals. The correlation of mean cavitation pressure and hydraulically weighted tracheid diameter across roots and branches of both species was significant; $r^2 = 0.58$ (Fig. 3).

During the summer drought, midday xylem pressures were as much as 1 MPa higher in *P. edulis* (to -2.4 MPa) than in *J. osteosperma* (to -3.5 MPa; Fig. 4). There were two reasons for this: (1) minimum predawn xylem pressures were higher in *P. edulis* (-1.8 MPa vs -2.8 MPa in *J. osteosperma*; Fig. 4) and (2) transpiration rates in *P. edulis* were reduced much more than in *J. osteosperma* as the drought progressed (Fig. 5a). The greater restriction of transpiration in *P. edulis* was associated with essentially constant midday xylem pressure regardless of the predawn pressure (Fig. 4). At a predawn pressure of -2 MPa, transpiration in *P. edulis* would be zero (Fig. 4, 5a). At the same pressure, transpiration in *J. osteosperma* was similar to pre-drought values for *P. edulis* (Fig. 5a).

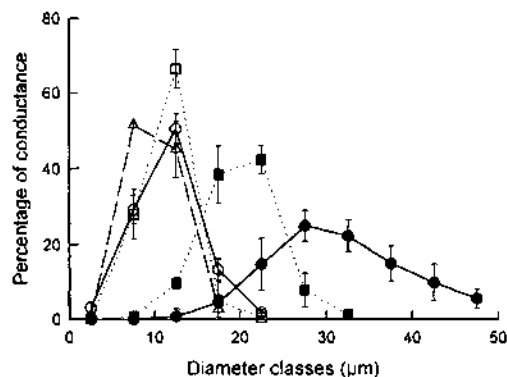


Fig. 2. Contribution of 5 μm tracheid diameter classes to total hydraulic conductance. Measurements were from the same plant segments as used in Fig. 1. *Pinus edulis* branches (\circ) and roots (\bullet), *J. osteosperma* adult branches (\square), roots (\blacksquare) and juvenile branches (\triangle). Error bars are SE.

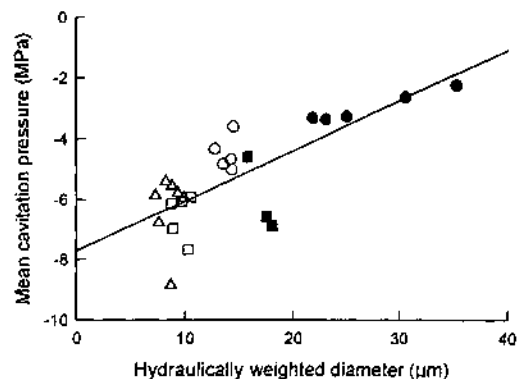


Fig. 3. Linear regression of mean cavitation pressure vs hydraulically weighted tracheid diameter. *Pinus edulis* branches (\circ) and roots (\bullet), *J. osteosperma* adult branches (\square), roots (\blacksquare) and juvenile branches (\triangle); $r^2 = 0.58$.

Although minimum xylem pressures were lower in *J. osteosperma* than *P. edulis*, the loss of hydraulic conductance during the drought was similar in both species. The predicted loss of conductance in roots increased from 9 to 28% in *P. edulis* and 1% to 17% in *J. osteosperma* over the summer: a 14–16% loss of conductance in each taxa from pre-drought values (Fig. 5b). Negligible loss of conductance ($< 3\%$) was predicted for stems. These small changes corresponded with no significant changes in measured whole-plant leaf-specific hydraulic conductance over the drought in either taxon ($r < 0.37$; $n = 23$).

If *P. edulis* had experienced the same range of transpiration and xylem pressure as *J. osteosperma*, the predicted loss of xylem conductance would be 55% in roots relative to pre-drought values (Fig. 5b, squares). Stems would show a modest 6% drop in conductance. Actual losses in conductance would probably be greater than this because of the positive feedback between decreasing hydraulic conductance and decreasing xylem pressure under transpirational conditions. The greater reduction of transpiration and higher predawn xylem pressure in *P. edulis* relative to *J. osteosperma* were necessary to avoid extensive cavitation of the root system.

Discussion

As predicted from its occupation of drier habitats, *J. osteosperma* was more resistant to xylem cavitation than *P. edulis* (Fig. 1). Within the range of xylem pressure measured in the field (0 to -3.5 MPa; Fig. 4), however, branches of the two species show similarly small hydraulic conductance losses (Fig. 1a). Only extremely severe drought that would cause stem xylem pressures to drop below -4 MPa would differentially cavitate branches of *J. osteosperma* and *P. edulis*. In contrast, the two species differed significantly in root cavitation over the same 0 to -3.5 MPa range, chiefly because roots of *P. edulis* were considerably more vulnerable than were branches (Fig. 1b).

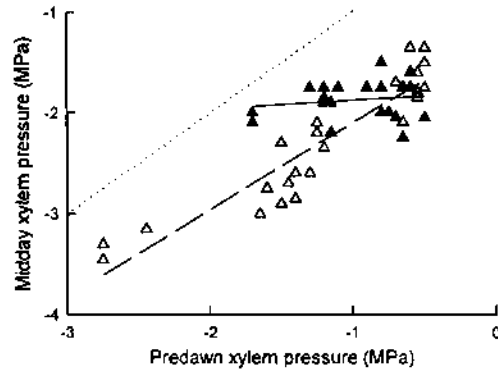


Fig. 4. Predawn vs midday shoot xylem pressure. Data is from May and August samplings across the four field sites. *Pinus edulis* (\blacktriangle), *J. osteosperma* (\triangle). Dotted line is 1:1.

These results suggest that root cavitation is more important than stem cavitation in determining the relative drought resistance of the two species. Roots also appear to be most limiting to cavitation resistance in *Pseudotsuga menziesii*, *Betula occidentalis*, *Acer grandidentatum* and a number of other species (Sperry & Saliendra 1994; Alder *et al.* 1996; Hacke & Sauter 1996; Sperry & Ikeda 1997).

It is important to realize that the most important consequence of cavitation is not necessarily the result of its occurrence but rather the result of its avoidance. In our study, little actual cavitation was predicted to

occur in either species, and whole-plant hydraulic conductances were statistically constant throughout the drought. The important point is that the pronounced stomatal closure in *P. edulis* and its higher predawn xylem pressure were necessary to avoid extensive root cavitation (Fig. 5). The stomatal conductance and range of soil water potential for *P. edulis* is hydraulically constrained relative to *J. osteosperma* because of the necessity of avoiding cavitation.

While *P. edulis* appeared to be operating near its hydraulic limits, the same was not the case for *J. osteosperma*. Mid-path xylem pressures could have dropped to -6 MPa before the xylem would become 50% cavitated (Fig. 1). From the hydraulic perspective, this species should be capable of growing in even more xeric sites than the typical habitats where it was studied. It is perhaps significant that with the advent of grazing pressure and reduced competition from palatable grasses and shrubs, and with a greater restriction of wildfire which kills *J. osteosperma*, the Juniper woodlands of the Great Basin have expanded in historical times to drier lower elevations previously dominated by shrubs and grasses (West 1988). The fact that juveniles of the species are equally resistant to cavitation as the adults (Fig. 1a) would facilitate this expansion into more arid habitat.

The results include some caveats. While we examined branch and root xylem, we only looked at one size class of each (diameters of roots 0.4–0.6 cm and branches 1.1–1.6 cm). A recent study of *Pseudotsuga menziesii* (Sperry & Ikeda 1997) found that the vulnerability of root xylem to cavitation increased with decreasing root diameter (to a minimum of 2 mm). The hydraulic constraints of the species studied here may have been under-estimated because the smaller roots were not examined. Finally, while we measured xylem pressure and transpiration across four widely spaced sites, we only quantified cavitation resistance at one of these sites. Although the Pinyon–Juniper habitat receives similar precipitation throughout the great basin (West 1988), it is possible that differences could exist in cavitation resistance across the species' ranges.

The results supported the existence of a trade-off between increasing hydraulic conductance (via larger diameter conduits) and decreasing cavitation resistance (Fig. 3). Nearly the identical result was also found for *Pseudotsuga menziesii* (Sperry & Ikeda 1997) and a trio of conifers in the north-eastern United States (Sperry & Tyree 1990). However, in a survey of several European conifers, Cochard (1992) found no consistent relationship between conducting efficiency and cavitation resistance. At the level of the interconduit pit, there is good reason to suspect a trade-off because a pit membrane that is less permeable to air entry should also be one less conductive to water. However, the overall conductance of the xylem is also dependent on the length and diameter of

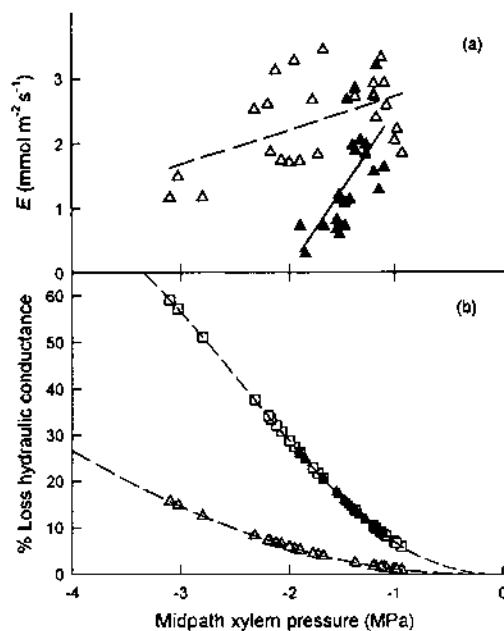


Fig. 5. (a) Midpath xylem pressure (halfway between midday and predawn xylem pressure) vs midday transpiration rate (E) for *P. edulis* (\blacktriangle) and *J. osteosperma* (\triangle). Data from May and August sampling dates across the four field sites. (b) Midpath xylem pressure vs percentage loss in root xylem conductance for *P. edulis* (\blacktriangle), *J. osteosperma* (\triangle), and *P. edulis* assuming *J. osteosperma* xylem pressures (\square). Dashed lines are root vulnerability curves from Fig. 1b, upper curve: *P. edulis*; lower curve: *J. osteosperma*.

the conduit itself, and the surface area of interconduit pit membranes. These factors can vary independently of individual pit membrane structure, thus potentially complicating the situation.

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